BODY INSULATION OF SOME ARCTIC AND TROPICAL MAMMALS AND BIRDS *

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Introduction

Since the early days of polar exploration it has been known that the arctic in the winter months supports a substantial population of mammals and birds and that these maintain a body temperature that falls within the normal limits found in temperate and tropical forms (Back, 1836; Parry and Lyon, 1825, 1827). All of these warm blooded animals, which include man, may at times be subjected to very low environmental temperatures. The coldest on record are − 68° C. in eastern Siberia and − 65° C. in northwestern Canada, with monthly averages running as low as − 60° C. and below − 50° C., respectively (Bartholomew and Herbertson, 1899; Court, Sissenwine and Mitchell, 1949).

This means for some animals the maintenance, for weeks, of a temperature gradient which may be as much as 100° between the interior of the body and the environment. Thermally this difference is equivalent to maintaining the animals at the boiling point of water in a zero degree environment. Both animals and man accomplish this by two principal adjustments: (1) by lowering the heat loss through increasing the insulation, and (2) by increasing the heat production through raising the metabolism. Actually the smaller mammals and birds, together with man, cannot endure the coldest weather continuously but escape, at least for their resting periods, by burrowing into the snow (ptarmigans), or into well insulated nests where they may stay close together (lemmings, mice, etc.), while others may retire under an electric blanket in a well heated hut (explorers). Finally, the hibernators (arctic ground squirrels) spend the winter within insulated burrows at a very low metabolic rate, just sufficient to maintain body temperature above freezing.

In the winters of 1947–48 and 1948–49, a number of species of arctic mammals and birds were captured near the laboratory at Point Barrow (lat. 71° N.), and were kept in outdoor cages in order to permit study of their means of adjustment to cold. At the same time a collection of winter furs was made.

It was considered that much might be gained in understanding adjustment to cold if we could extend our investigation to include tropical mammals and birds. Through the courtesy of the Navy it was possible to undertake such an investigation during three months in Panama at the U. S. Naval Air Station, Coco Solo, Canal

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Zone, and three months at the Canal Zone Biological Area (Barro Colorado Island), at latitude 9° N.

In the present paper we shall deal with observations on factors that influence the heat loss from the animal, especially the insulation afforded by the fur and feather covering, as measured in pieces of raw skin and fur taken directly from the skinned animal. The arctic furs were all in prime winter condition. Naturally such measurements can only give a rough estimate of how the body insulation varies from one species to another. The living animal may vary the fur and skin insulation greatly by erecting the hairs, by vasomotor control of the skin and tissue temperature immediately under the fur, by changes in evaporation, etc. There are also considerable regional differences in heat loss of body, legs, and face. Respiration and posture of the animal likewise are major factors in determining the total heat loss. Even the relative figures obtained from such skin patch measurements could be misleading as to the total insulation of the animal. We could easily imagine a chubby arctic animal with short, well insulated legs and tail to have a better overall insulation than a tropical animal with long, poorly insulated arms, legs, and tail, even though the tropical form might have a better body insulation than the arctic form.

In spite of these limitations, it was considered that representative insulation measurements of the furs from a series of mammals from the arctic and the tropics would be indispensable for an analysis of the temperature sensitivity in the living species.

The importance of the natural fur and feather covering as an insulator has been long appreciated (Bergmann, 1847; Rubner, 1924; Lefevre, 1911; Tigerstedt, 1910), but few quantitative data on the subject (Giaja, 1931; Babenyscheff, 1938) have been found.

Material

Raw skins were secured from the following arctic mammals, all caught in the winter except the shrew:

Shrew (*Sorex tundrensis*)
Grizzly bear (*Ursus* sp.)
Polar bear (*Thalarctos maritimus*)
Marten (*Martes americana*)
Least weasel (*Mustela rixosa*)
Red fox (*Vulpes fulva alascensis*)
White fox (*Alopex lagopus*)
Eskimo dog (*Canis familiaris*)
Dall sheep (*Ovis dalli*)
Wolf (*Canis lupus*)
Seal (*Phoca hispida*)
Ground squirrel (*Citellus parryi*)
Beaver (*Castor canadensis*)
Lemming (*Dicrostonyx groenlandicus rubricatus*)
Lemming (*Lemmus trimucronatus*)
Hare (*Lepus americanus*)
Reindeer (*Rangifer*—domesticated)
Caribou (*Rangifer arcticus*)

Fat and pieces of musculature were removed from the raw hide and the hair side was carefully dried. The flesh side was left naturally moist for the measurements. Except for a thermally insignificant localized fat pad on the rump of the reindeer and caribou, none of the mammals (except the seals) has any significant layer of subcutaneous fat or blubber. Subcutaneous fat is a heavy and poor insulator compared to fur and does not seem to play any role at all in the insulation of terrestrial arctic mammals. In the aquatic seals and whales, however, it is the principal or only insulating material. In the seals the skin with blubber adhering to it was detached from the underlying muscle fascia.

Skins from the following tropical mammals were secured in the Panama Canal Zone:

Opossum (*Didelphis marsupialis*)
Night monkey (*Aotus trivirgatus*)
White-faced monkey (*Cebus capucinus*)
Marmoset (titi) (*Leontocebus geoffroyi*)
Three-toed sloth (*Bradypus griseus* or *ignavus*)
Two-toed sloth (*Choloepus hoffmanni*)
Rabbit (*Sylvilagus gabbi*)
Squirrel (*Sciurus granatensis* or *variegatoides*)
Jungle rat (*Proechimys semispinosus*)
Paca (*Cuniculus paca*)
Agouti (*Dasyprocta punctata*)
Raccoon (*Procyon cancrivorus* or *lotor*)
Coati (*Nasua narica*)
Kinkajou (*Potos flavus* or *Bassaricyon gabbi*)
Collared peccary (*Tayassu angulatus*)
Deer (*Mazama sartorii*)

Patches of raw hide large enough for insulation measurements were cleaned, dried, and shipped with disinfectant to the Point Barrow laboratory where the flesh side was remoistened before the measurement. The skin patches were later sent to the Smithsonian Institution, where they were kindly identified by Dr. David H. Johnson and Dr. H. W. Setzer.

Insulation Measurement

The heat transmission through the fur was measured by employing a conventional hot plate and guard ring technique. The hot plate was made of two circular aluminum discs with an insulated hot wire spiral between them. A similarly constructed guard ring, as wide as the radius of the plate, surrounded the center plate. The plate and guard ring could be independently heated and their temperatures read by thermocouples attached to the metal surfaces. The heating of the guard ring could be controlled with sufficient accuracy by a variac; the center plate was heated from a storage battery and the energy input was measured by an ammeter and a voltmeter.

Three sizes of such hot plate guard ring units were employed with the hot plate, 6, 3, and 1 $dm.^2$ in area, respectively, depending upon the thickness and size of the skin samples to be measured. Covered with pieces of uniform celotex, the three plates gave a heat transfer reading per unit surface within 3 per cent of each other, and within 5.5 per cent of the figure reported for celotex in the *Handbook of Chemistry and Physics,* 29, p. 1822.

For the measurement, two similar skin pieces (usually from either side of the back on the same animal, or from the backs of two smaller animals) were stretched flat by means of thumbtacks over a circular hole in two plywood frames. The hot plate unit, placed in a flat thin cellophane bag, was sandwiched between the moist flesh sides of the skins and the frames were clamped together (Fig. 1).

To make the measurement, the frame with skins and hot plate unit was hung up vertically in a room thermostabilized at 0° C. ± 1°. The plate and guard ring were heated to 37° C. and held there until the energy input had reached a constant minimum, indicating that heat saturation and equilibrium between heat input and heat loss had been reached. A heavy skin usually required two to three hours before

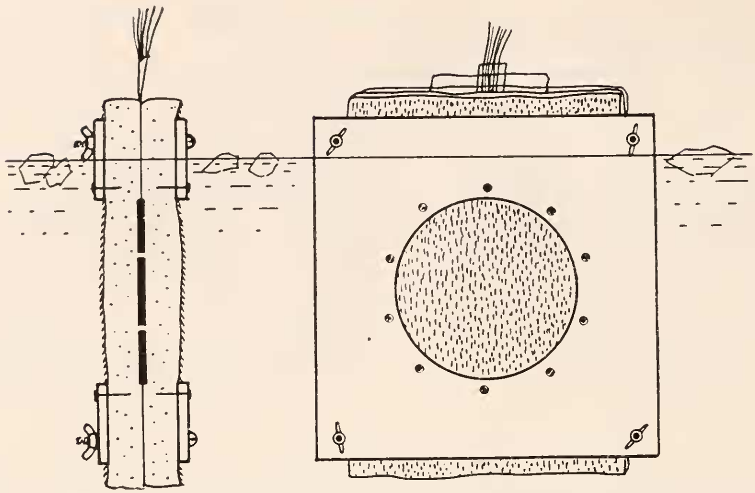

FIGURE 1. Method for measurement of heat transfer through seal skin and blubber in ice water. Left, cross-section through plywood frames holding slabs of seal blubber, clamped around the hot plate guard ring unit. Right, frontal view. Nails are driven through the frame around the center hole to hold the heavy blubber in place. Measurements of the skin of land animals were made with the frame suspended in air at 0° C.

reaching equilibrium. The determinations were made with the fur ruffed up as much as possible for maximum insulating values.

Among arctic animals the insulation of the fur is so large that the hide comprises a relatively small part of the total insulation. The thermal gradients observed in the fur of white fox and caribou showed the surface temperature of the skin to be substantially lower than that of the plate (Fig. 2). This is caused by some ex-

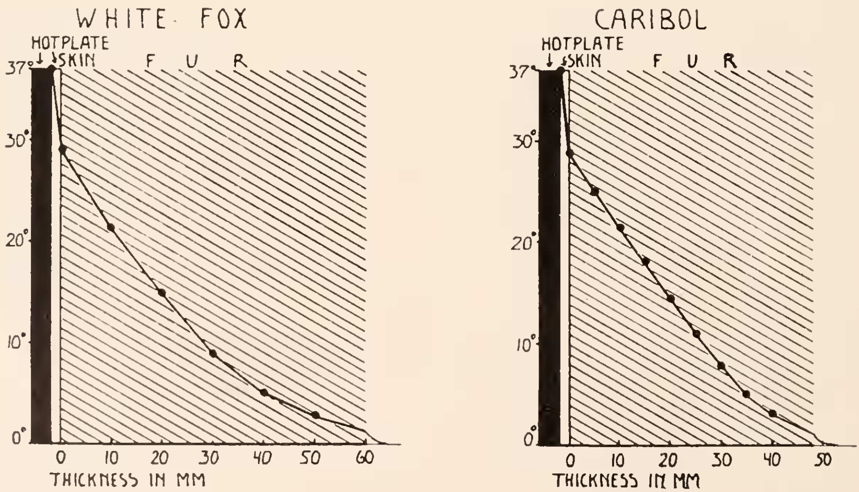

FIGURE 2. Thermal gradients set up in fur of white fox and caribou when in position on the hot plate.

traneous factor, possibly evaporation or poor contact between plate and skin, as it is reasonable to believe that the skin is a poorer insulator than the fur. The decrease in slope of the temperature gradient in the outer layers of the fox fur arises from superficial thinning of the fur. Caribou fur is uniformly dense right to the surface.

In the samples from tropical animals, which often have sparse and short fur, most of the insulation noted in these tests was actually afforded by the hide. This undoubtedly makes the insulation values found for tropical animals considerably higher than in life, when the hide is vascularized, serving heat dissipation rather than heat conservation. In practically naked animals, like the peccary and the paca, the insulation of the fur must be near zero.

Measurement of thickness of the fur is naturally quite arbitrary. A blunt needle was pushed through the fur against the skin and the more or less well defined main surface of the fur set off on the needle with the thumb and measured in millimeters. The average of several such measurements was taken to represent the thickness of the fur.

Insulation in Mammals

The heat transfer was measured in watts per dm.^{2} per 37° C. temperature gradient and the insulation is given as the reciprocal of the heat transfer.[5]

In Figures 3 and 4, observed insulation values are correlated with the thickness of the fur. As was to be expected there is a close correlation with the thickness. None of the furs, under the circumstances tested, were quite as good insulators as an equally thick layer of medium dense cotton. Some of the polar bear furs were conspicuously open and coarse haired and proved to be poor insulators for their thickness.

Among mammals the size of the fox or larger, there is no clear correlation of fur thickness or insulation to the size of the animal (Fig. 5). At the size of the fox, insulation seems to have reached a useful maximum shared by most of the larger forms, including man wearing eskimo parka and pants made of one layer of caribou or other fur. With size decreasing below that of the fox, fur must be shorter and lighter or the animal could not move about. This is particularly true for the smallest forms, the shrew, weasel, and lemming. The ground-squirrels are somewhat out of line, with very little insulation compared to weight. However, they are hardly ever exposed to such gradients as the others, since they escape into their burrows and hibernate. At the lower end of the scale we note that small arctic mammals overlap in insulation value some of the tropical forms, which is a remarkable fact. We shall see, however, that arctic and tropic forms are nevertheless quite different in their temperature sensitivity.

Eskimo dogs and white and red foxes were observed to sleep unprotected on the snow at − 50° C., and so presumably do the wolves, polar bears, caribou, Dall sheep, and other large mammals. The smaller mammals, however, all live in burrows in the winter time and have insulated nests of grass, cotton grass, reindeer

[5] Professor Alan C. Burton has kindly informed us that this unit of insulation amounts to about 2.4 Clo units, and that the slope of the fur insulation in Fig. 3 works out at about 3.7 Clo per inch, which is the accepted value for still air in clothing. An arctic uniform has about 5 Clo units or about 35 mm. thickness. It will be noted that this is considerably less than what most of the larger arctic mammals wear on their body.

hair, etc. Their habits supplement the meager insulation of their fur. As will be shown later, their metabolic heat regulation has already set in before the temperature drops to zero, so that whenever they leave their nests in cold weather they have to be active in order to maintain their body temperature. At Point Barrow the snow temperature at ground level usually stayed at − 25° C. during the winter. One

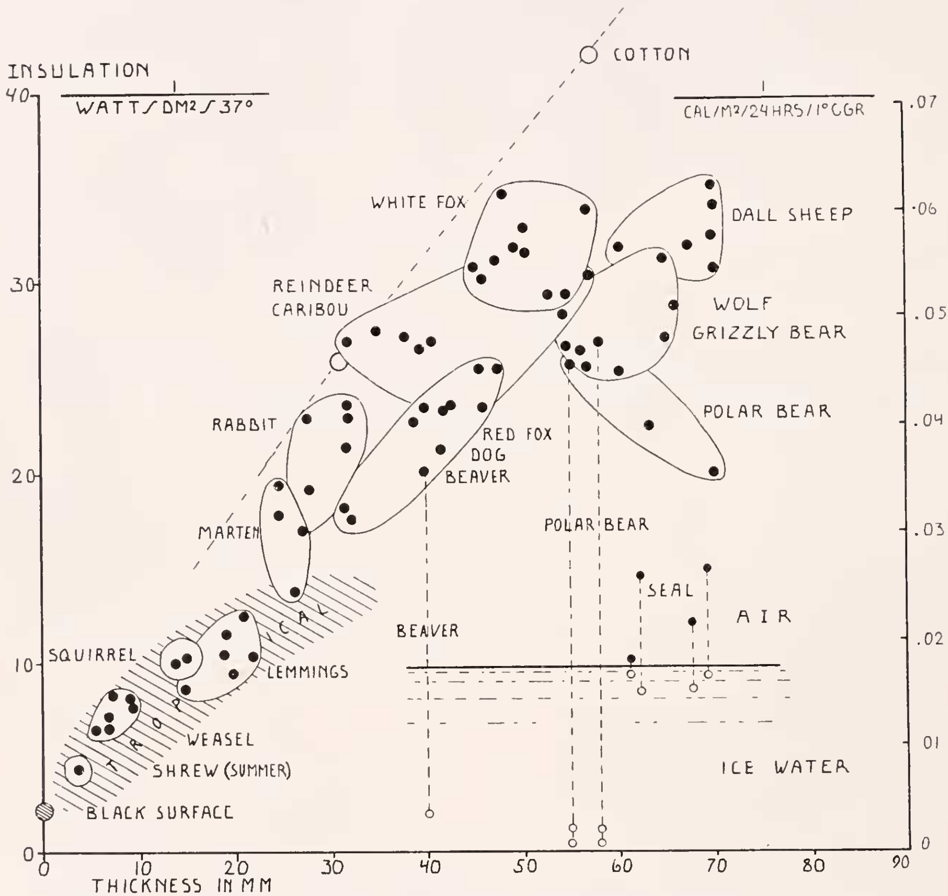

FIGURE 3. Insulation in relation to winter fur thickness in a series of arctic mammals. The insulation in tropical mammals is indicated by the shaded area. In the aquatic mammals (seal, beaver, polar bear) the measurements in 0° C. air are connected by vertical broken lines with the same measurements taken in ice water. In all cases the hot plate guard ring unit was kept at 37° C. and the outside air or water at 0° C. The two upper points of the lemmings are from *Dicrostonyx*, the others from *Lemmus*.

small lemming nest of grass was found in fair condition after the spring thaw and showed an insulating value of the walls, in air, roughly 1.5 times that of the lemming fur. Covered with snow, the insulation could have been no less. Colonial nests, which are much larger, have been observed and it is reasonable to believe that the nests are warm enough to maintain an air temperature around the animals at + 10°

C. or better, which is their critical temperature. Below 10° C. they would have to raise their metabolic rate.

The shrew, weighing only 1.9 gm., was found in the summer time, and its skin was too small to be measured on the smallest hot plate. The insulation of the summer skin has been estimated from its fur thickness. As in the other animals, its insulation is probably greater in winter.

Among the tropical mammals tested (Fig. 4), the sloths are the best insulated, which seems to be necessitated by their low rate of metabolism. The kinkajou and

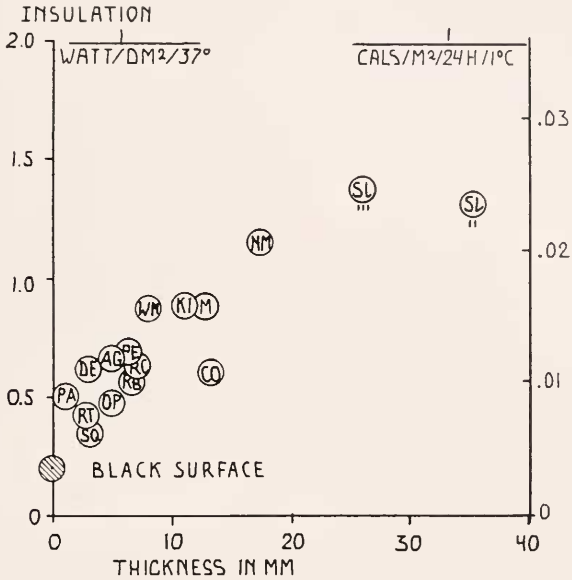

Figure 4. Insulation in relation to fur thickness in tropical mammals. Hot plate guard ring unit 37° C., outside air 0° C. The insulation of the fur of most of these animals is probably close to that of a bare black surface but is higher in our measurements because of the relative high insulation of the skin in our dead samples.

AG—agouti
CO—coati
DE—deer
KI—kinkajou
M—marmoset
NM—night monkey
OP—opossum
PA—paca
PE—peccary
RB—rabbit
RC—raccoon
RT—rat
SL II—2-toed cloth
SL III—3-toed sloth
SQ—squirrel
WM—white-faced monkey

night monkey, both active nocturnal and arboreal mammals, are relatively well insulated, whereas other nocturnal ground mammals like the paca, opossum, and jungle rat are among the poorest insulated. There does not appear to be any correlation between insulation and diurnal or nocturnal habits. If anything, it would seem that a night sleeper, passive when it is coldest, might need more insulation than a day sleeper. But the microclimates selected are not known. It should not be forgotten that in many boreal, as well as tropical climates, almost naked mammals live side by side with relatively furry mammals, pointing to the potency of peripheral vasomotor control for the regulation of the body insulation.

Among the smaller arctic mammals like the lemming, weasel, and snow-shoe rabbit, the legs and feet have a considerable fur protection as compared with their southern relatives. However, among the birds that will withstand cold winters, naked legs are most common, and legs insulated with feathers, as in the ptarmigan and snowy owl, are exceptions. In general the insulation on the legs and feet in mammals and birds is very much less than on the body. Several measurements on mountain sheep, caribou, and reindeer showed only from $1/5$ to $1/3$ as much insulation

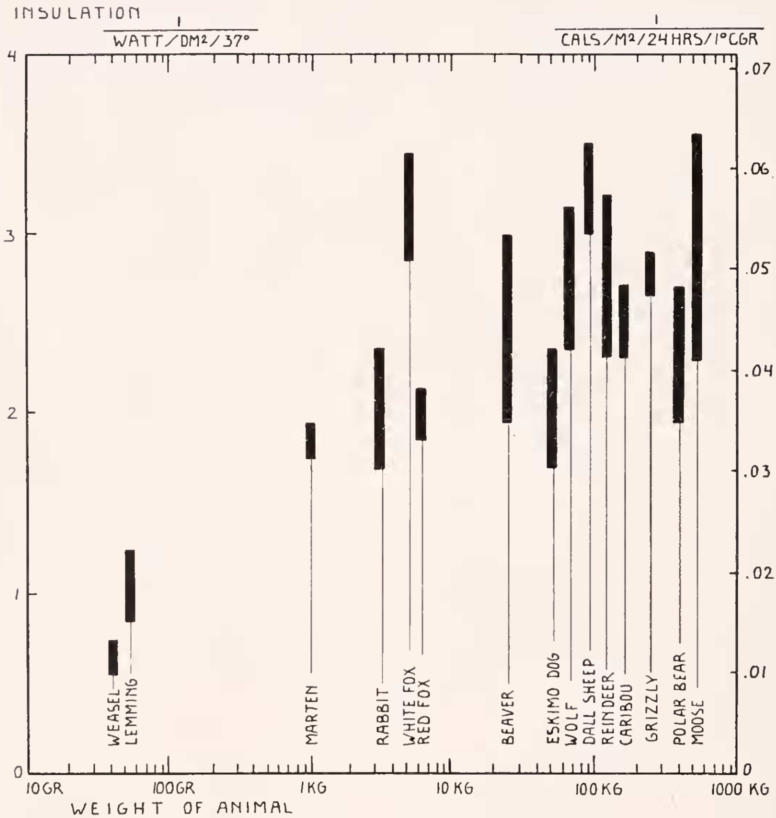

FIGURE 5. Insulation of the winter fur in relation to the body weight in a series of arctic mammals. From a 5 kg. fox to a 500 kg. moose the insulation does not vary much in most of the animals.

on the legs as on the body. We know that aquatic birds can stand low leg temperatures. Undoubtedly seals, muskrats, beavers, moose, and other semi-aquatic mammals can also stand low leg temperatures for a long time, as they virtually lack insulation against the ice water. It seems very probable that arctic nonaquatic mammals and birds can also stand prolonged low leg temperatures because the leg insulation is so slight. This assumption is strongly supported by measurements of the melting point of fats taken from caribou legs. Thus Abrahamsen (1950) found that fats taken from the lower parts of the legs had a melting point thirty degrees lower than that of fats from the upper parts of the legs. If poorly circulated the legs would cool and further heat loss would be retarded. Fully circulated, the legs would become warm and would greatly facilitate heat loss on account of their poor insulation. This may, in part, explain the fact that a resting, heavily insulated arctic mammal or bird is nevertheless able to change its heat dissipation by a factor of eleven times. By pilo motor reflex alone it seems doubtful whether a caribou or fox could even double its insulation. The fur of a lemming fluffed up to the maximum, provided roughly only twice as much insulation as the fur with the hairs smoothed down.

Insulation in Birds

Insulation measurements were made on snow bunting and ptarmigan skins. The snow buntings gave figures comparable to those of the lemmings and the ptarmigan figures were comparable to those of the marten. However, these measurements are less satisfactory since it is impossible to produce on the test plate the well-ordered elevation of the feathers which the live bird can achieve to produce maximum insulation.

Our snow buntings spent the winter standing on the board floor in their outdoor wire cage with temperatures often as low as $-40°$ C. Only in the coldest weather did these birds, ravens and gulls, find it necessary to protect their naked feet by sitting on them. Only a few of the buntings showed evidence of frostbite on their slender naked feet. A dozen arctic gulls walked about all winter on the snow in an outdoor wire cage with temperatures sometimes as low as $-50°$ C. without freezing their large-surfaced naked webbed feet. A few determinations of the heat dissipation from a live gull's feet in ice water showed it to be very low. It corresponded to only a few cc. of blood an hour, indicating that the temperature of the foot and leg must have been close to zero. Such a low leg temperature can evidently be tolerated for hours at a time and results in general heat conservation for the bird. None of our gulls froze their feet. The circulation must have increased with the increasing gradient so as to keep the feet and legs at just above freezing; and it is likely that the heat loss from the legs and feet, below freezing, increases linearly with the gradient. A gull that had been kept indoors for several months, in a cage usually warmer than 20° C., was observed to freeze the web on its feet, white and hard, in less than one minute after it escaped through an open door onto the snow outside at $-20°$ C. The outer web and parts of some toes subsequently became gangrenous and were lost. Evidently it had lost its cold adaptation or its vaso motor response was not quick enough.

Insulation Measurements in Aquatic Mammals

In man even a few minutes of partial or total immersion in ice water causes unbearable chill and pain, and yet some arctic mammals spend all or parts of their lives swimming about in icy, subzero waters. It is, therefore, of interest to know something about their body insulation in ice water as compared with that in air. Insulation measurements in ice water were made on skins from the polar bear, beaver, and seal (*Phoca hispida*). This species of seal spends most of its life in waters around 0° C. and possesses only a thin hair covering, but it has a thick layer of blubber

(Fig. 6). The blubber is only sparsely vascularized. When the seal submerges the water penetrates the fur completely, leaving no insulating air layer between the skin and the water.

In a series of experiments the heat transmission through the skin and blubber, when submerged in ice water, was measured (Fig. 3). Similarly, the heat losses in ice water through polar bear skin and beaver skin were measured. It can be seen that seal fur and blubber is not a good insulator in air, only slightly better than

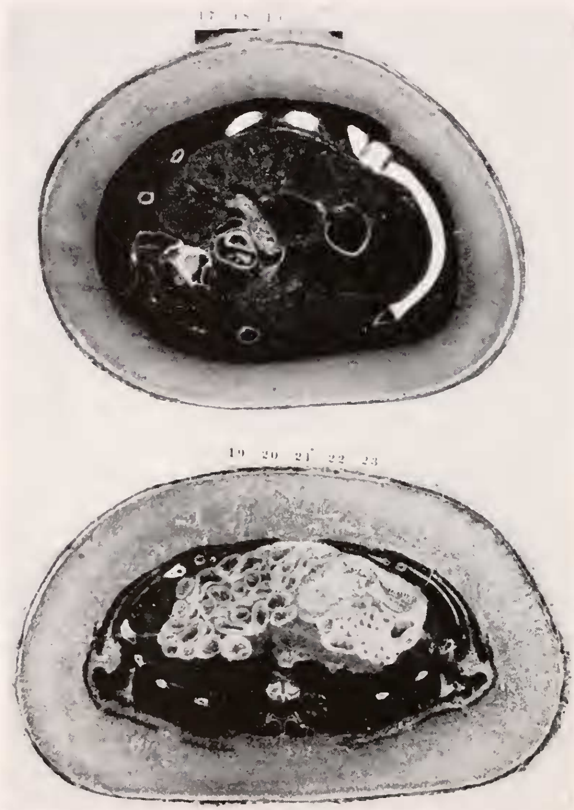

FIGURE 6. Cross sections of two frozen seals (*Phoca hispida*) shot in March, 1948, showing the thick layer of blubber. Tape measure in inches.

that of a lemming, although more than three times as thick. The effectiveness of blubber as an insulator in water is demonstrated by the fact that in one of the seal specimens tested, the insulation in ice water was only 5 per cent less than in zero degree air, which means that the temperature gradient in air and in ice water was taken up almost completely within the blubber, leaving the skin surface correspondingly cool in either medium. In all observations the insulation in ice water was about the same, and the difference from the insulation in air can most likely be ascribed to differences in the fur cover. In a living seal the insulation of the skin and blubber is undoubtedly even less than in our samples because of some subcutaneous and cutaneous circulation. It must be remembered, however, that as long as the seal is in water the temperature gradient is always moderate, never over 40°. Furthermore, the seal is a bulky animal with a high metabolic rate (Irving, Solandt, Solandt and Fisher, 1935; Scholander, 1940). It has in its flippers a highly effective vasomotor control (Scholander, 1940; Irving, Scholander and Grinnell, 1941), and it can readily be seen how even a slight increase in the peripheral circulation could remove large quantities of heat generated by swimming.

In contrast to the seal, the heat loss through polar bear skin increases 20–25 times when submerged in quiet ice water, and 45–50 times when the water is agitated. The ice water penetrates immediately to the skin surface, dislodging all air, and there is no subcutaneous blubber to afford insulation. Undoubtedly, therefore, the polar bear upon immersion suffers a considerable heat loss at the skin surface. This is probably reduced by peripheral vasoconstriction and cooling and can apparently be compensated for over a long time by heat production during swimming. The coarse and open polar bear fur sheds water very easily upon shaking, so that the insulation is readily restored when the bear emerges. The polar bear is also a very large animal with large heat capacity and has a proportionately small surface.

In contrast to the seal and polar bear, the beaver has an extraordinarily dense and fine fur which retains a layer of air several millimeters thick next to the skin when submerged. This can be easily observed on a submerged skin sample. It undoubtedly helps the insulation, which nevertheless is surprisingly low in ice water.

Summary

Insulation measurements on raw skins from 16 arctic and 16 tropical mammals are given. There is, as would be expected, a good correlation between the thickness of the fur and the insulation. The smaller arctic mammals (weasels, lemmings) have much less insulation than the larger and overlap many of the tropical forms. From the size of a fox to the size of a moose there is no correlation between insulation and body size, they all have about the same insulation per surface area. When submerged in ice water, seal blubber retains about the same good insulation, as compared with measurements taken in 0° C. air. In the polar bear, heat transfer through the fur increases 25–50 times when submerged, because of complete wetting of the skin surface and absence of blubber. The beaver is slightly better off when submerged, as it retains an insulating layer of air in the fur next to the skin.

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